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SYNOPSIS AND POLLEN MORPHOLOGY OF VERNONIA (COMPOSITAE: VERNONIEAE) IN THE NEW WORLD

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The tribe Vernonieae was recognized by Cassini (1817, 1819) and delimited by Lessing (1829, 1831a & b). Lessing's organization was used by de Candolle (1836) to form the basis of his classification. The next major reorganization was that of Bentham (1873) and Bentham and Hooker (1873). In 1894, Hoffman made a few rearrangements, but his treatment is essentially the same as Bentham's. Smaller, but important, contributions have been made by several workers who have examined and classified portions of the tribe on a limited geographical basis, e.g. Schultz-Bipontinus (1861, 1863), Baker (1873), Gleason (1906, 1922), Ekman (1914), and Cabrera (1944).

The tribe has over 1,450 species and about 70 genera, with ca. 37 genera being monotypic. *Vernonia*, the largest genus in the tribe, with ca. 900 to 1,000 species, is predominately tropical. Four to five hundred species of *Vernonia* are native to the New World with about the same number in Africa and southeast Asia. *Vernonia* forms the central core of the Vernonieae with the smaller genera appearing to radiate from it. Although the importance of *Vernonia* to the classification of the tribe is clear, there has been no comprehensive reevaluation of the genus since de Candolle (1836) and Bentham (1873). Subsequent changes in its classification generally have been restricted to limited geographic areas. The current delimitation of sections, subsections, series, etc., of *Vernonia* is nebulous and many are clearly artificial (Smith, 1971).

Vernonia presents an impressive array of leaf and stem morphology, habit, and ecological preference, demonstrating the tremendous diversification that has occurred during its evolution. The habit of *Vernonia* varies widely. Some species are annuals; others

are perennial herbs, shrubs, or trees. The plants range in size from acaulescent perennials ca. 4 cm tall to trees reaching 30 m in height. They inhabit a wide array of habitats. A few species grow in marshy or wet soil, others in very dry places. Some *Vernonias* inhabit cloud forests, additional ones are adapted to grassland-fire habitats. In spite of this radiation, many of the reproductive features of *Vernonia* have remained remarkably constant. In addition to the diversification, parallelism is rampant when species grow in similar habitats.

Since evolution of the group has often caused species relationships to become obscured, it is difficult to arrange phylogenetic groupings and construct a classification. In addition, since the genus is so large and accommodates so much variation and parallelism, subdivisions of the genus above the rank of species have been difficult to circumscribe fully. To achieve a higher level of clarity, additional characters must be used to aid in developing an improved classification. Both Gleason (1923) and Cabrera (1944) have pointed out the possible value of inflorescence types as a character in *Vernonia*.

Figures 1-3 show generalized representative inflorescences of *Vernonia* in the New World. **1f**, **2c**, **2e**, **2f**, & **2g** follow Cabrera (1944), and **2d** follows Gleason (1923). All are drawn or redrawn from herbarium material. The presence or absence of bracteal leaves subtending the heads is significant.

Another such character is external pollen morphology (Fig. 4). Workers such as Wodehouse (1928), Smith (1969), Jones (1970), Kingham (1976), and Keeley and Jones (1977) have demonstrated the variability and usefulness of pollen features of *Vernonieae*. In the last few years, evidence from two additional sources has been accumulating slowly, i.e., natural plant products (Mabry, et al., 1975) and chromosome numbers (Jones, 1977). It seems likely that new evidence from pollen morphology, chemosystematics, and cytotaxonomy, when combined with evidence from gross morphology, can be used to improve the classification of *Vernonia*.

The present investigation is based upon some 16 years experience in the genus and includes field work in the United States, Mexico, and Brazil, along with greenhouse and garden studies. In addition, two months were spent in England at K and BM. During the past several years, the pollen grains of over 600 species of *Vernonia* were acetolyzed by the procedure of Erdtman (1966) and prepared for

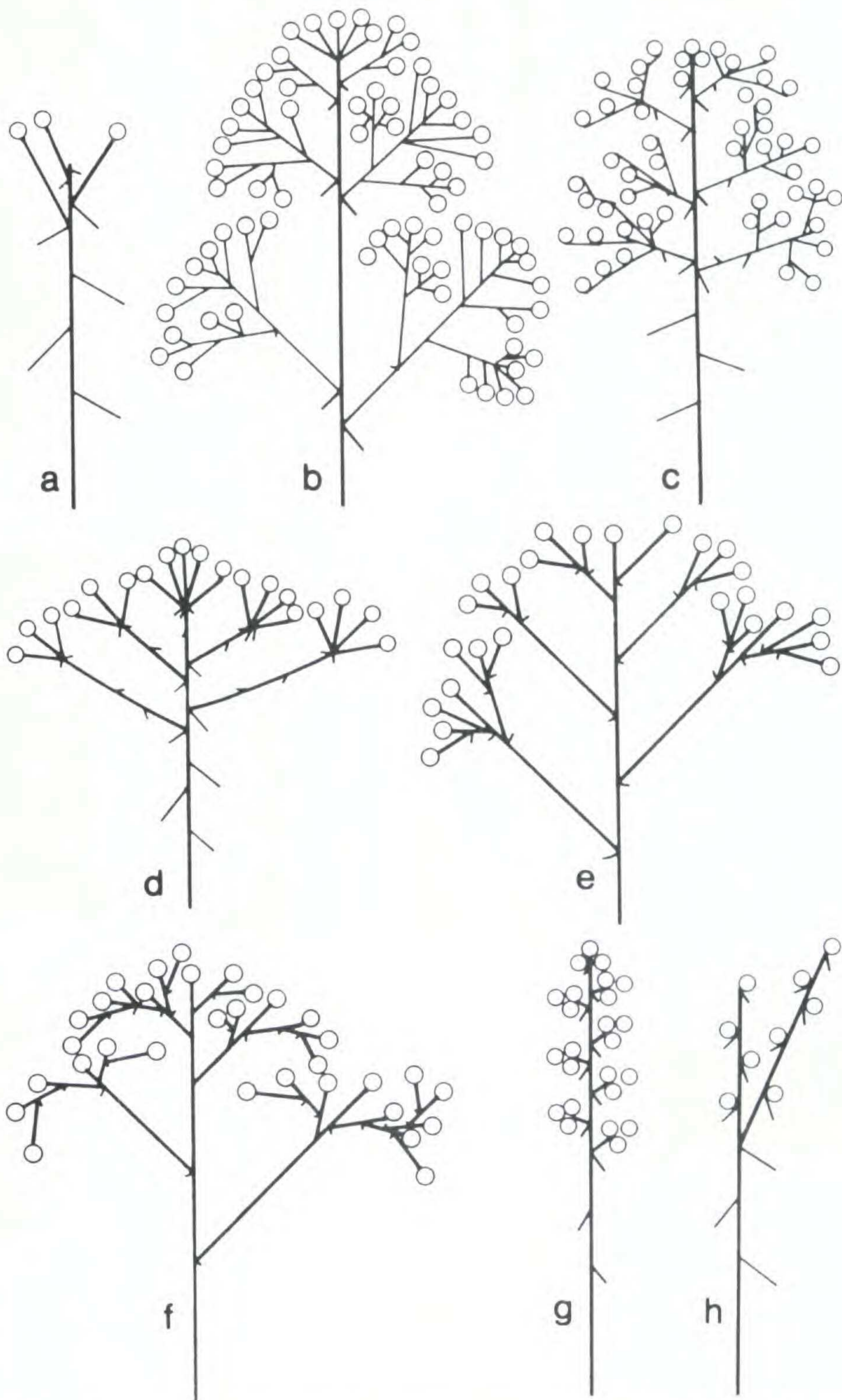


Figure 1. Generalized representative inflorescences of *Vernonia* in the New World. If follows Cabrera (1944).

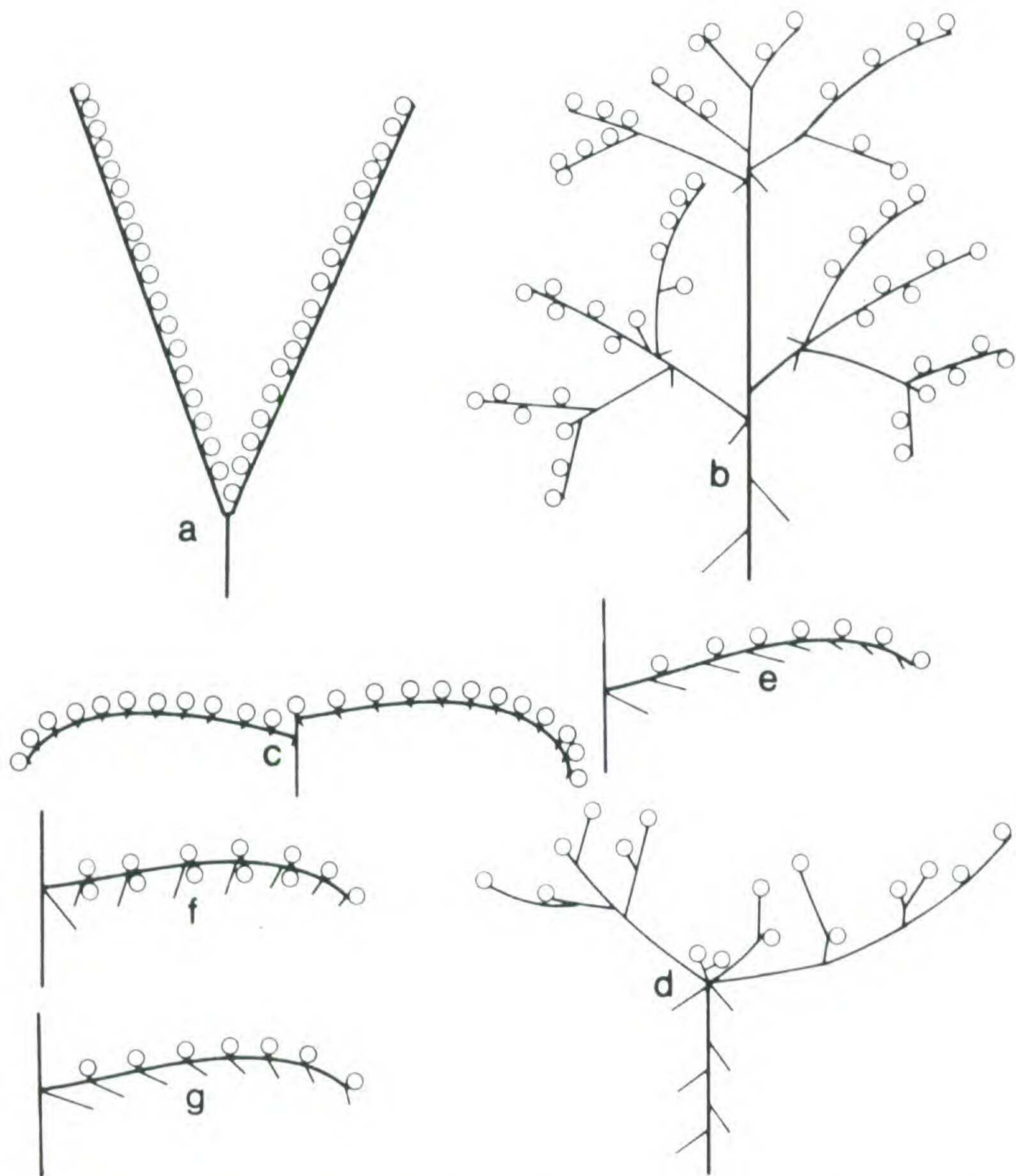


Figure 2. Generalized representative inflorescences in *Vernonia* in the New World. 2c, e, f, & g follow Cabrera (1944). 2d follows Gleason (1923).

light microscopy by mounting whole grains in glycerin jelly on glass slides and staining them lightly with methyl green. Acetolyzed grains were prepared for scanning electron microscopy (SEM) as previously described by Jones (1970). Light microscopy supplemented by SEM was used to determine the pattern of the grains. Names of the species cited in the paper are those taken from labels unless an obvious error was detected. In such cases, the sheets were annotated.

Once the pollen type had been determined, attempts were made to develop phylogenetic groupings using other available data. In the process, it became apparent that the best approach was to report the results of the pollen study in conjunction with a synoptic treatment. Four types of pollen grains are known from the New World *Vernonias* (Fig. 4). In addition, two other types of pollen grains not known from the New World are found in the Old World. The results are then summarized here, but due to the size of the genus this paper treats only the New World *Vernonias*, which are recognized as belonging to a subgenus erected on morphological, chemical, and cytological grounds. The New World *Vernonias* have chromosome numbers based on $n = 17$, whereas $n = 9$ and 10 in the Old World (Jones, 1977). Likewise, the sesquiterpene lactones of the New World *Vernonias* are similar to but differ from those found in the Old World (Mabry, et al., 1975). The Old World species will be treated in a second paper.

The major goal of the effort was to develop a classification which reflects evolution. Furthermore, the development of phylogenetic units provides workable-sized groups of species for taxonomic

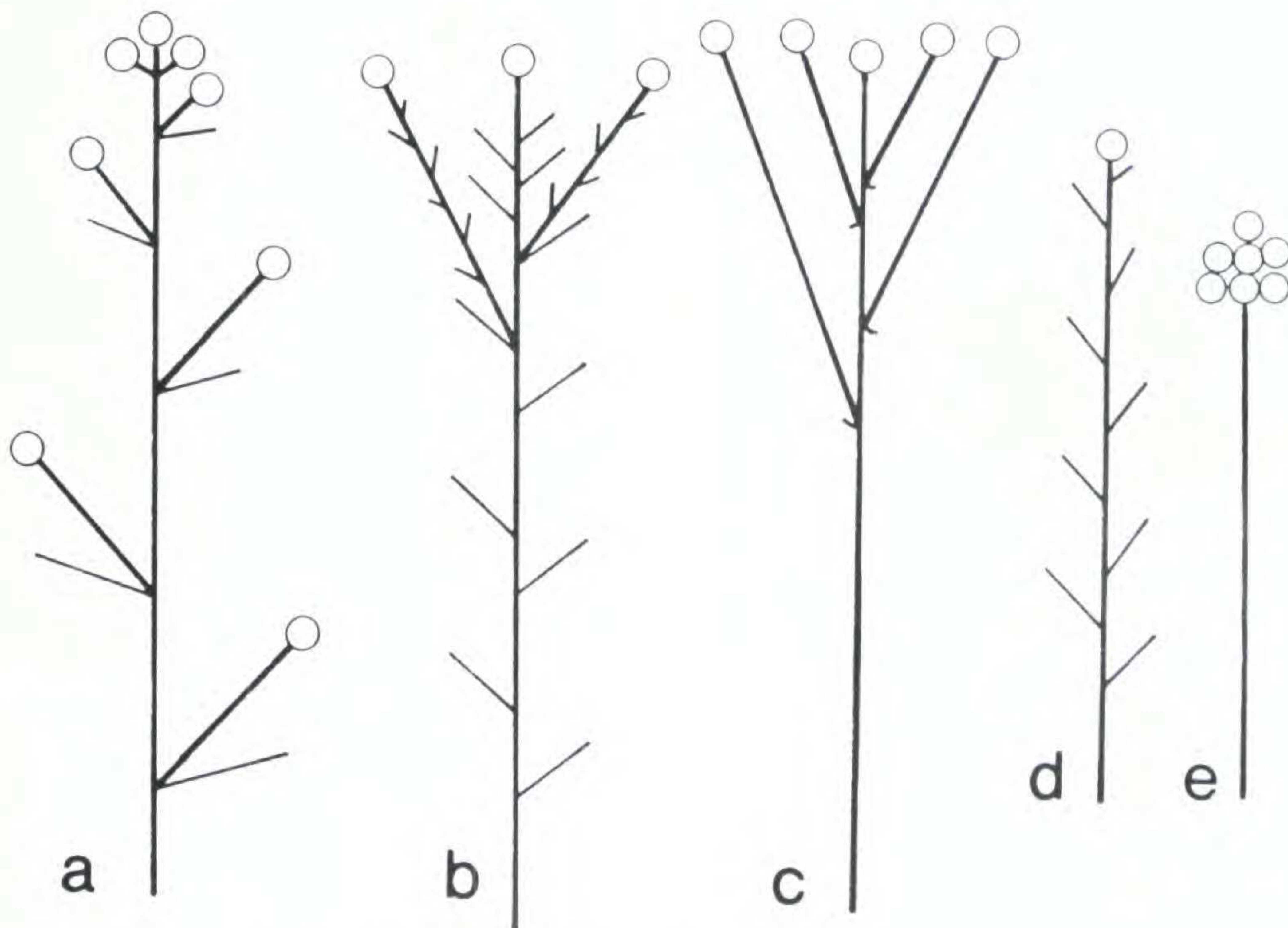


Figure 3. Generalized representative inflorescences of *Vernonia* in the New World.

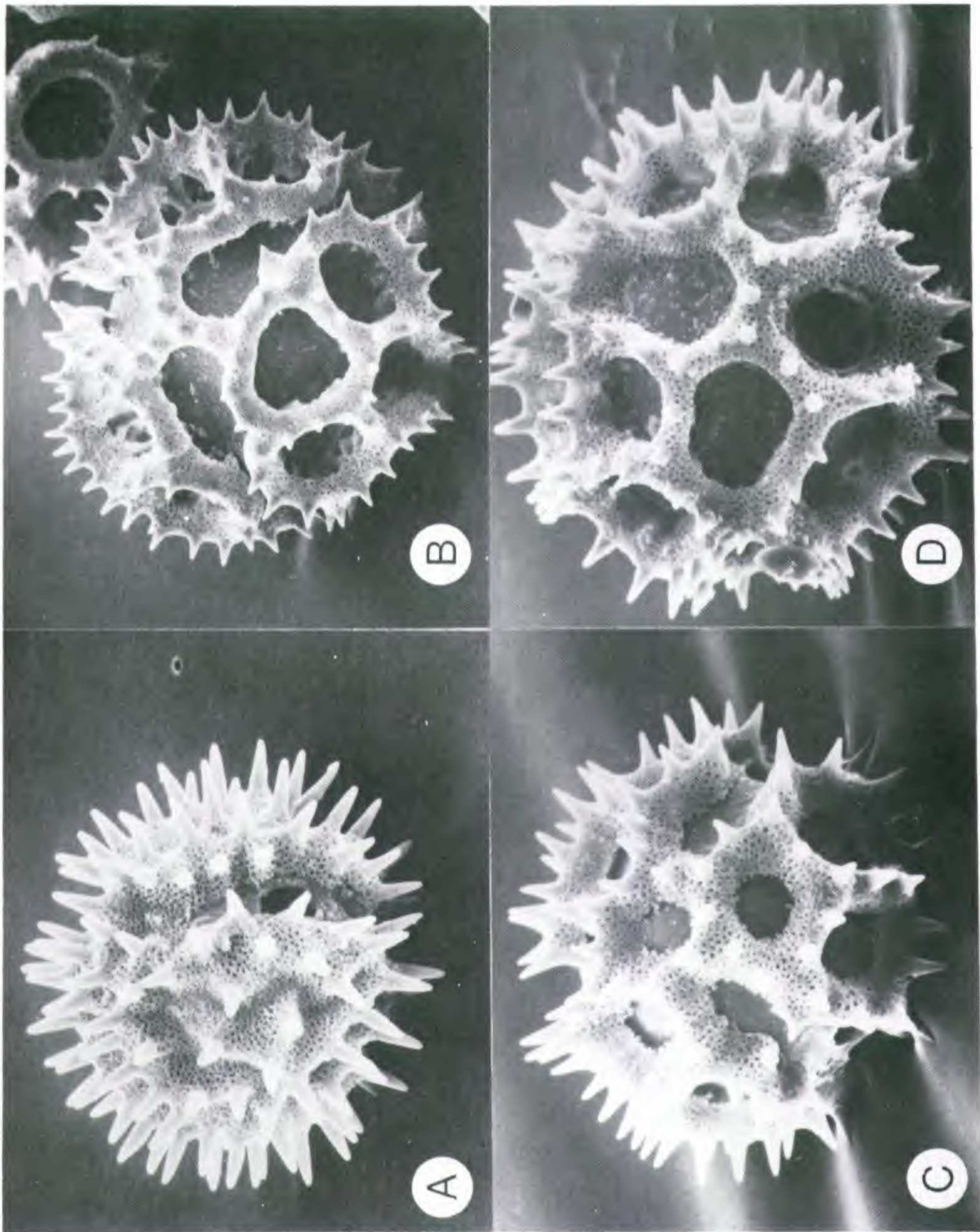


Figure 4. Pollen types A, B, C, and D of *Vernonia* from the New World. Type A: *V. barkerii*, equatorial view, diameter of grain ca. 44 μm . Type B: *V. amorphila*, polar view, diameter of grain ca. 66 μm . Type C: *V. canescens*, polar view, diameter of grain ca. 44 μm . Type D: *V. eremophylla*, equatorial view, diameter of grain ca. 56 μm . Types A, B and C were described in Keeley and Jones (1977). Type D has a ridge surrounding the germinal pore, and therefore, lacks a germinal furrow. Type A is regarded as primitive and types B, C, and D as derived. Spines are sometimes reduced to almost absent in types B and C.

revision. Undoubtedly, with additional study, some groups presented here will have to be redefined. Until an effort is made to develop a new classification, the genus will stand in the arrangements of the 1800s.

SYNOPSIS OF CLASSIFICATION OF THE NEW WORLD VERNONIAS:

Vernonia

Subgenus *Vernonia*

Section *Leiboldia*

Section *Hololepis*

Section *Vernonia*

Subsection *Noveboracenses*

Subsection *Eremosis*

Subsection *Polyanthes*

Subsection *Buxifoliae*

Subsection *Chamaedrys*

Subsection *Stenocephalum*

Subsection *Nudiflorae*

Series *Nudiflorae*

Series *Brevifoliae*

Series *Verbascifoliae*

Series *Subulatae*

Subsection *Scorpioides*

Series *Scorpioides*

Series *Macrolepidae*

Series *Remotiflorae*

Series *Flexuosae*

Series *Aureae*

Series *Canescentes*

Series *Foliatae*

Series *Sagraeanae*

Series *Arborescentes*

Series *Pallescentes*

Subgenus **Vernonia**. TYPE SPECIES: *Vernonia noveboracensis* (L.) Willd.

Herbaceous perennials to shrubs and small trees; inflorescences highly variable, forming complex patterns often based upon a scorpioid-cymose design sometimes greatly reduced, in others very

large (Figs. 1, 2 & 3); heads with 1 to numerous florets; involucre usually campanulate, phyllaries usually tightly appressed; pappus usually in two series, and occasionally subequal; corollas reddish-purple to pinkish or whitish, never bright blue nor yellow in color.

Geographical distribution: from Manitoba, Canada and the eastern United States, Mexico, and the West Indies south into Argentina. Most abundant in southern Brazil and the mountains of Mexico, Central America, and the Andes.

Chemistry: the new world species thus far examined all contain the glaucolide type of sesquiterpene lactone.

Chromosome numbers: based upon $n = 17$.

Pollen types: A, B, C, and D (Fig. 4).

Section **Leiboldia** (Schlecht.) Benth. & Hook. Gen. Pl. **2**: 228. 1873.

Leiboldia Schlecht. Linnaea **19**: 742. 1847. TYPE SPECIES: *Vernonia leiboldiana* Schlecht.

Shrubs or small trees; leaves elliptic to lanceolate or obovate; inflorescences terminal, of a few heads, often arranged in the axils of foliage leaves (see Fig. 1a); heads large and with numerous florets; phyllaries lanceolate to semi-foliaceous; pappus bristles subequal in several series; corollas with tubes twice as long as the lobes.

Geographical distribution: mountains of southern Mexico into Central America.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia arctioides Less., MÉXICO: Oaxaca, *Smith 4495* (US). **V. corae** Standl. & Steyerl., GUATEMALA: San Marcos, *Williams, et al. 25943* (NY). **V. mexicana** Less., MÉXICO: Puebla, *Sharp 45806* (NY).

Section **Hololepis** (DC.) DC. Prodr. **5**: 16. 1836.

Hololepis DC. Ann. Mus. Nat. Hist. Paris **16**: 190. 1810. TYPE SPECIES: *Vernonia pedunculata* (DC.) DC.

Woody shrubs; leaves ovate, coriaceous above, tomentose beneath; inflorescences of single heads borne in axils of upper foliage leaves (see Fig. 1a); heads large, with numerous florets, phyllaries in two distinct series, the outer ovate and leaf-like, the inner smaller and lanceolate; pappus of subequal bristles; corolla lobes twice the length of the tube; achenes glabrous, faintly ribbed.

Geographical distribution: in the state of Minas Gerais, Brazil.

Pollen type: A. Pollen grains were examined from the following specimen:

Vernonia pedunculata DC., BRAZIL: Minas Gerais, Irwin, et al. 30242 (NY).

Section **Vernonia** TYPE SPECIES: *Vernonia noveboracensis* (L.) Willd.

Section *Lepidaploa* (Cass.) DC. Prodr. 5: 26. 1836.

Section *Stenocephalum* (Sch.-Bip.) Benth. & Hook. Gen. Pl. 2: 230. 1873.

Section *Trianthaea* Spach. Hist. Veg. Phan. 10: 39. 1841.

Section *Critoniopsis* (Sch.-Bip.) Benth. & Hook. Gen. Pl. 2: 230. 1873.

Section *Eremosis* (DC.) Benth. & Hook. Gen. Pl. 2: 231. 1873.

Shrubs, small trees, herbaceous perennials, rarely annuals; pappus usually in two distinct series.

Geographical distribution: from extreme southern Canada south into Argentina. The greatest number of species are found in southern Brazil, the West Indies, Mexico and the eastern United States.

Chemistry: sesquiterpene lactones of a glaucolide type.

Chromosome numbers: a series based on $n = 17$, with $n = 17$, 34, 51, and 68.

Pollen types: A, B, C, and D.

Subsection **Noveboracenses** Ekman, Ark. Bot. 13(15): 95. 1914.

TYPE SPECIES: *Vernonia noveboracensis* (L.) Willd.

Herbaceous perennials, sometimes becoming slightly woody at base; leaves highly variable; inflorescences corymbose to paniculate (see Figs. 1b, 1d, 2d); heads of 10 to 60 florets; phyllaries small, outer greatly reduced; pappus bristles in two series, outer pappus often scale-like; achenes usually ribbed.

Geographical distribution: much of the eastern United States, and into southern Manitoba, Canada, southward to southern Mexico.

Chemistry: sesquiterpene lactones glaucolide-A, B, F, and marginata.

Chromosome number: $n = 17$.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia acaulis (Walt.) Gleason, UNITED STATES: Georgia, *Duncan 12029* (GA). **V. alamanii** DC., MÉXICO: Michoacan, *Jones 22407* (GA). **V. angustifolia** Michx., UNITED STATES: Alabama, *Kral 28542* (GA). **V. arkansana** DC., UNITED STATES: Arkansas, *Demaree 59216* (GA). **V. autumnalis** McVaugh, MÉXICO: Jalisco, *McVaugh 25476* (GA). **V. baldwini** Torr., UNITED STATES: Oklahoma, *Jones 15850* (GA). **V. bealliae** McVaugh, MÉXICO: Jalisco, *McVaugh 10331* (NY). **V. blodgettii** Small, UNITED STATES: Georgia, *Jones 1099* (GA). **V. cronquistii** S. B. Jones, MÉXICO: Guerrero, *Cronquist 11226* (GA). **V. fasciculata** Michx., UNITED STATES: Iowa, *Urbatsch 33* (GA). **V. flaccidifolia** Small, UNITED STATES: Georgia, *Urbatsch 99* (GA). **V. gigantea** (Walt.) Trel., UNITED STATES: Georgia, *Urbatsch 125* (GA). **V. glauca** (L.) Willd., UNITED STATES: Georgia, *Holder 1929* (GA). **V. greggii** Gray, MÉXICO: Nuevo Leon, *Chapman 82* (GA). **V. karvinskiana** DC., MÉXICO: Oaxaca, *Jones 21669* (GA). **V. larsenii** King & Jones, UNITED STATES: Texas, *Demaree 58832* (GA). **V. lettermanni** Engelm., UNITED STATES: Arkansas, *Jones 15838* (GA). **V. liatroides** DC., MÉXICO: México, *Jones 22389* (GA). **V. lindheimeri** Gray & Engelm., UNITED STATES: Texas, *Jones 15877* (GA). **V. marginata** (Torr.) Raf., UNITED STATES: Oklahoma, *Jones 17670* (GA). **V. missurica** Raf., UNITED STATES: Arkansas, *Jones 15831* (GA). **V. noveboracensis** (L.) Michx., UNITED STATES: Georgia, *Jones 1201* (GA). **V. oaxacana** Sch.-Bip. ex Klatt, MÉXICO: Oaxaca, *Jones 21670* (GA). **V. pulchella** Small, UNITED STATES: Georgia, *Jones 1085* (GA). **V. serratuloides** H.B.K., MÉXICO: Najavit, *Hennen 238* (GA). **V. texana** (Gray) Small, UNITED STATES: Mississippi, *Jones 17657* (GA).

Subsection **Polyanthes** Ekman, *Ark. Bot.* **13**(15): 89. 1914. TYPE SPECIES: *Vernonia baccharoides* H.B.K.

Woody shrubs to suffrutescent perennials; inflorescences paniculate to corymbose to semi-scorpioid cymose (see Figs. 1b, 1c, 1d, & 1f); heads usually medium sized with ca 15–25 florets; phyllaries usually small and tightly imbricate; achenes usually ribbed.

Geographical distribution: southern Mexico south through Central America and down the Andes into Brazil.

Chromosome number: $n = 17$.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia aschenborniana Schauer, MÉXICO: Veracruz, *Ventura A. 5040* (NY). **V. baccharoides** H.B.K., PERU: San Martín, *Belshaw 3242* (F). **V. bakerana** Britt., BOLIVIA, *Buchtien 1546* (NY). **V. crotonides** Sch.-Bip., BRAZIL: Minas Gerais, *Irwin, et al. 29689* (NY). **V. deppeana** Less., MÉXICO: Jalisco, *McVaugh 22912* (NY). **V. discolor** Less., BRAZIL, *Lanna 1823* (GA). **V. ferruginea** Less., BRAZIL: Mato Grosso, *Ratter & de Castro 117* (NY). **V. fulva** Griseb., ARGENTINA: Tafi, *Sás 174* (NY). **V. havanensis** DC., CUBA, *Barker & Abarco 3721* (US). **V. hieracioides** Griseb., CUBA, *Morton & Acuna 3120* (US). **V. jubifera** Rusby, BOLIVIA, *Bang 1554* (NY). **V. menthaefolia** (Poepp.) Less., CUBA, *Wright (1860-64) 2792* (MO). **V. oppositifolia** Less., BRAZIL, *Sobrinho 1817* (GA). **V. pacchensis** Benth. var. *tambillensis* Hieron., PERU: Piura, *Hutchinson & Wright 6690* (MO). **V. patens** H.B.K., PERU: San Martín, *McDaniel 14232* (GA). **V. petiolaris** DC., BRAZIL, *Lejo 16117* (NY). **V. polyanthes** (Spreng.) Less.,

BRAZIL: Minas Gerais, *Williams & Assis 8010* (GA). **V. polylepsis** Sch.-Bip., PERU: Cuzco, *Vargas 2038* (MO). **V. rubriramea** Mart. ex DC., BRAZIL: Minas Gerais, *Pires 57961* (NY). **V. ruficoma** Schlecht. ex Mart., BOLIVIA, *Williams 1410* (NY). **V. sordidopapposa** Hieron., PERU: Cuzco, *Vargas C. 15495* (NY). **V. stellaris** Llave & Lex., COSTA RICA, *Molina R., et al. 18006* (NY). **V. suaveolens** H.B.K., ECUADOR: Cañar, *Prieto P-76* (NY). **V. trichoclada** Gleason, PERU: Cuzco, *Vargas 6083* (F).

Subsection **Eremosis** (DC.) S. B. Jones, *stat. nov.*

Monosis DC., Section *Eremosis* DC. Prodr. **5**: 77. 1836. TYPE SPECIES: *Vernonia salicifolia* (DC.) Sch.-Bip. (*Monosis salicifolia* DC.).

Critoniopsis Sch.-Bip. Pollichia **20/21**: 430. 1863.

Section *Critoniopsis* (Sch.-Bip.) Benth. & Hook. Gen. Pl. **2**: 230. 1873.

Shrubs or small trees; inflorescences large, paniculate (see Figs. 1b & 1d); heads sessile, subsessile, or sometimes pedicellate, few (1–16) flowered; phyllaries in several series, inner usually deciduous; pappus of bristles, outer pappus shorter, variable, and sometimes lacking.

Geographical distribution: Sierra Madre Orientale and Occidentale of Mexico south through Central America, then along the Andes into Brazil.

Chemistry: sesquiterpene lactones glaucolide-A, B, C, D, E, F, G, and H.

Chromosome number: $n = 17$.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia baadii (McVaugh) Jones, MÉXICO: Michoacan, *Hinton, et al. 13651* (NY). **V. barbinervis** Sch.-Bip. ex Seem., MÉXICO: Sinaloa, *Jones 22530* (GA). **V. bogotana** Cuatr., COLOMBIA: Cundinamarca, *Fosberg & Villareal 20575* (NY). **V. glandulata** Cuatr., COLOMBIA: Del Norte de Santander, *Fosberg 19154* (NY). **V. gurigaseusis** Britt., BOLIVIA, *Rusby 1732* (NY). **V. leiocarpa** DC., MÉXICO: Chiapas, *Jones 21675* (GA). **V. littoralis** Brandeg., MÉXICO, *Moran 5760* (NY). **V. obtusa** Blake, MÉXICO: San Luis Potosí, *Cronquist 11274* (GA). **V. pallens** Sch.-Bip., MÉXICO: Michoacan, *McVaugh 22556* (NY). **V. paniculata** DC., MÉXICO: Michoacan, *Jones 22401* (GA). **V. pycnantha** Benth., ECUADOR, *Espinosa 1572* (NY). **V. salicifolia** (DC.) Sch.-Bip., MÉXICO: México, *Jones 20571* (GA). **V. shannoni** Coult., GUATEMALA: Totonicapán, *Williams, et al. 22913* (NY). **V. steetzii** Sch.-Bip., MÉXICO: Jalisco, *Jones 20583* (NY). **V. tarchonanthifolia** (DC.) Sch.-Bip., MÉXICO: Oaxaca, *Cronquist 10908* (GA). **V. triflosculosa** H.B.K., MÉXICO: Oaxaca, *Jones 21671* (GA). **V. uniflora** Sch.-Bip., MÉXICO: México, *Jones 22390* (GA).

Subsection **Buxifoliae** Ekman, Ark. Bot. **13**(15): 22. 1914. TYPE SPECIES: *Vernonia buxifolia* (Cass.) Less.

Series *Aggregatae* Gleason. Bull. New York Bot. Gard. **4**: 190. 1906.

Woody, rigid shrubs; leaves coriaceous; inflorescences terminal and cymose, of few (3–5) heads (see Figs. 1b & 1g); heads small with ca 10 florets; achenes glabrous with 8–9 ribs.

Geographical distribution: A distinct subsection from Hispaniola.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia barkeri Ekman, HISPANIOLA, *Ekman 7351* (US). **V. buxifolia** (Cass.) Less., HISPANIOLA, *Ekman 3391* (GH). **V. tuerckheimii** Urban, HISPANIOLA, *Keeley & Keeley 1489* (GA).

Subsection **Chamaedrys** Cabrera, *Darwiniana* 6: 307. 1944. TYPE SPECIES: *Vernonia chamaedrys* Less.

Subsection *Nitidulae* Cabrera, *Darwiniana* 6: 347. 1944.

Fruticose perennials to shrubs; inflorescences cylindrical, compact, thyrsoid-paniculate (see Figs. 1b, 1g, & 1e); heads numerous, medium sized with 10–20 florets; phyllaries tightly imbricated in several series.

Geographical distribution: from Peru south to Argentina, but centered in southern Brazil. A well marked and distinctive subsection.

Chromosome number: $n = 17$.

Pollen types: A and B. Pollen grains were examined from the following specimens:

(TYPE A) **Vernonia chamaedrys** Less., BRAZIL: Paraná, *Hatschbach 31764* (NY). **V. chaquensis** Cabrera, ARGENTINA: Mburucuyá, *Peterson 1708* (NY). **V. crassa** Ekman ex Malme, BRAZIL: Paraná, *Lindemann & De Haas 2452* (NY). **V. cuneifolia** Gardn., BRAZIL: Paraná, *Lindemann & DeHaas 5537* (NY). **V. flex** Chod., PARAGUAY, *Hassler 3800* (NY). **V. florida** Gardn., BRAZIL: Paraná, *Hatschbach 30290*, (NY). **V. gochnatioides** Hook. & Arn. ex DC. URAGUAY: Colonia, *Cabrera 3882* (NY). **V. jalcana** Cuatr., PERU: Amazônas, *Hutchinson & Wright 5515* (MO). **V. laxa** Gardn., PARAGUAY, *Hassler 9136* (NY). **V. montevidensis** (Spring) Ekman, ARGENTINA, *Rodriguez 37* (NY). **V. mucronulata** Less., BRAZIL: Minas Gerais, *Williams & Assis 1486* (GA). **V. nitidula** Less., BRAZIL: Paraná, *Hatschbach 22424* (NY). **V. oligactoides** Less., BRAZIL: Paraná, *Dusén 9680* (NY). **V. oligolepis** Sch.-Bip., BRAZIL: Paraná, *Dusén 9192* (NY). **V. puberula** Less., BRAZIL: Paraná, *Hatschbach 20081* (NY). **V. quinqueflora** Less., BRAZIL: Santa Catarina, *Reitz & Klein 9702* (NY). **V. rigiophylla** Sch.-Bip. ex Baker in Mart., BRAZIL: Paraná, *Reiss 43A* (NY). **V. squamulosa** H. & A., ARGENTINA: Tucumán, *Sás 93* (NY). **V. viscidula** Less., BRAZIL: Minas Gerais, *Pieres 57938* (NY).

(TYPE B) **Vernonia myrsitnitis** Ekman, BRAZIL: Goiás, *Ana 519* (NY). **V. pycnostachya** DC., BRAZIL: Minas Gerais, *Irwin, et al., 27655* (NY). **V. rosea** Mart. ex DC., BRAZIL: São Paulo, *Brade 20635* (NY). **V. tomentella** Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 20341* (NY). **V. vepretorum** Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 22619* (NY).

Subsection **Stenocephalum** (Sch.-Bip.) S. B. Jones, *stat. nov.*

Stenocephalum Sch.-Bip. *Pollichia* **20/21**: 385. 1863. TYPE SPECIES: *Vernonia apiculata* Mart. ex DC.

Annuals or herbaceous perennials; leaves densely white pubescent beneath; heads cylindric, elongate, small with 4–12 florets, sessile, sometimes clustered or arranged in axils of leaves (see Figs. 2f & 2g); phyllaries apiculate; achenes pubescent.

Geographical distribution: Mexico south to and centered in southern Brazil, sometimes weedy.

Chromosome number: $n = 17$.

Pollen type: C. Pollen grains were examined from the following specimens:

Vernonia apiculata Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al.* 26921 (NY). **V. hexantha** Sch.-Bip. ex Baker in Mart., PARAGUAY, *Hassler* 9825a (NY). **V. jucunda** Gleason, MÉXICO: Chiapas, *Breedlove & Raven* 13724 (NY). **V. megapotamica** Spreng., ARGENTINA: Mburucuyá, *Petersen* 1380 (NY). **V. tragiaefolia** DC., BRAZIL: São Paulo, *Brade* 5711 (NY).

Subsection **Nudiflorae** Cabrera, *Darwiniana* **6**: 353. 1944. TYPE SPECIES: *Vernonia nudiflora* Less.

Herbaceous perennials, sometimes woody at base, rarely annuals; leaves linear to elliptic or lanceolate; inflorescences corymbose-paniculate to reduced and few-flowered; heads small to medium sized or sometimes large.

Geographical distribution: southern Brazil to Argentina.

Series **Nudiflorae** S. B. Jones, *ser. nov.*

Herbae perennes vel raro suffrutices; caules simplices vel raro ramosi; folia linearia vel lanceolata; inflorescentiae corymboso-paniculatae vel diminutae; capitula 10–25 flosculis. TYPE SPECIES: *Vernonia nudiflora* Less.

Herbaceous perennials, sometimes slightly woody at base; leaves frequently linear, sometimes elliptic or lanceolate; inflorescences corymbose-paniculate or reduced (see Figs. 1b, 1c, 1e, 1f, 3a, & 3e); heads small to medium sized with 10–25 florets.

Geographical distribution: southern Brazil south into Argentina.

Chemistry: Sesquiterpene lactones glaucolide-A and B.

Chromosome number: $n = 17$.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia amplexicaulis Fries, ARGENTINA: Jujuy, *Venturi 5218* (NY). **V. amygdalina** Lam., BRAZIL: Goiás, *Irwin, et al. 17827* (NY). **V. brasiliana** Druce., BRAZIL, *Bunting 3343* (GA). **V. densiflora** Gardn., BRAZIL: Paraná, *Hatschbach 16239* (NY). **V. echioides** Less., BRAZIL: Paraná, *Hatschbach 30991* (NY). **V. incana** Less., ARGENTINA: Empedrado, *Pederson 9613* (NY). **V. lorentensis** Hieron., ARGENTINA: Mburucuyá, *Petersen 1442* (NY). **V. marianna** Mart., BRAZIL: Minas Gerais, *Irwin, et al. 28388* (NY). **V. missionis** Gardn., BRAZIL: Minas Gerais, *Macedo 2346* (NY). **V. nudiflora** Less., URUGUAY, *Millot 11362* (GA). **V. pseudo-linearifolia** Hieron., PARAGUAY, *Hassler 3654* (NY). **V. scabra** Pers., BRAZIL: Goiás, *Irwin, et al. 17793* (NY). **V. scapigera** Baker ex. Mart., BRAZIL: Minas Gerais, *Irwin, et al. 28085a* (NY). **V. tweediana** Baker ex. Mart., PARAGUAY: Guairé, *Pedersen 10094* (NY). **V. westiniana** Less., BRAZIL: São Paulo, *Filho 75-1* (GA).

Series **Brevifoliae** (Cabrera) S. B. Jones, *stat. nov.*

Subsection *Brevifoliae* Cabrera, *Darwiniana* 6: 303. 1944. TYPE SPECIES: *Vernonia brevifolia* Less.

Herbaceous perennials; leaves usually linear but sometimes elliptic to ovate; inflorescences greatly reduced, sometimes corymbose (see Figs. 3a, 3b, 3c, & 3d); heads relatively few to typically solitary.

Geographical distribution: southern Brazil south into Argentina.

Chromosome number: $n = 17$. Series *Brevifoliae* is very closely related to series *Nudiflorae*.

Pollen types: B and D. Pollen grains were examined from the following specimens:

(TYPE B) **Vernonia compactiflora** Mart. ex Baker in Mart., BRAZIL: Distrito Federal, *Irwin, et al. 13155* (NY). **V. erythrophila** DC., BRAZIL: Distrito Federal, *Irwin, et al. 10064* (NY). **V. graminifolia** Gardn., BRAZIL: Minas Gerais, *Irwin, et al. 28405* (NY). **V. grandiflora** Less., PARAGUAY, *Hassler 4341* (NY). **V. hypochaeris** DC., BRAZIL: Paraná, *Lindeman & de Haas 2526* (NY). **V. intermedia** DC., URUGUAY, *Rosengurt B-2401* (NY). **V. psilophylla** DC., BRAZIL: Minas Gerais, *Irwin, et al. 28090* (NY). **V. sessilifolia** Less., BRAZIL: Paraná, *Hatschbach 15959* (NY).

(TYPE D) **Vernonia brevifolia** Less., BRAZIL: Paraná, *Lindeman & de Haas 3091* (NY).

Series **Verbascifoliae** S. B. Jones, *ser. nov.*

Herbae perennes vel suffrutices; inflorescentiae diminutae; capitula magna, 40–80 flosculis; phyllaria magna. TYPE SPECIES: *Vernonia verbascifolia* Less.

Herbaceous perennials, sometimes becoming woody at base; leaves tomentose and often conspicuously whitish beneath; inflorescences often greatly reduced with few heads, sometimes branched

and having several heads (see Figs. 1f, 1g, 1h, 3a, 3b, 3c, & 3d); heads large and conspicuous with 40 to 80 florets; phyllaries relatively large, often tightly overlapping.

Geographical distribution: southern Brazil south to Argentina.

Chromosome number: $n = 17$.

Pollen type: B. Pollen grains were examined from the following specimens:

Vernonia argentea Less., BRAZIL, *Loëfgrun 16103* (NY). **V. argyrophylla** Less., BRAZIL: Minas Gerais, *Jones 22665* (GA). **V. asteriflora** Mart., BRAZIL: Paraná, *Hoehne 23391* (NY). **V. buddleiaefolia** Mart. ex DC., BRAZIL: Goiás, *Irwin, et al. 25019* (NY). **V. farinosa** Baker in Mart., BRAZIL: Minas Gerais, *Irwin, et al. 23247* (NY). **V. flavescens** Glaziou, BRAZIL: Goiás, *Anderson 10287* (NY). **V. floccosa** Gardn., BRAZIL: Goiás, *Anderson 10117* (NY). **V. lorentzii** Hieron., ARGENTINA: Federación, *Pedersen 4720* (NY). **V. mollissima** D. Don ex Hook. & Arn., PARAGUAY, *Hassler 9227a* (NY). **V. monocephala** Gardn., BRAZIL: Goiás, *Irwin, et al. 24711* (NY). **V. secunda** Sch.-Bip. ex Baker in Mart., BRAZIL: Distrito Federal, *Irwin, et al. 15459* (NY). **V. venosissima** Sch.-Bip. ex Baker in Mart., BRAZIL: Distrito Federal, *Irwin, et al. 15642* (NY). **V. verbascifolia** Less., BRAZIL: Minas Gerais, *Irwin, et al. 19668* (NY). **V. warmingiana** Baker in Mart., BRAZIL: Minas Gerais, *Irwin, et al. 25490* (NY).

Series **Subulatae** S. B. Jones, *ser. nov.*

Herbae annuae vel perennes; caules diffusi vel infirme ramosi inflorescentiae corymboso-paniculatae vel diminutae; capitula pusilla, 10–20 flosculis; phyllaria lanceolata. TYPE SPECIES: *Vernonia subulata* Baker.

Annuals or herbaceous perennials, diffuse or weakly branched; leaves relatively small, linear-lanceolate to elliptic-lanceolate; inflorescences corymbose-paniculate to reduced and sparingly branched (see Figs. 1b & 3a); heads relatively small with 10–20 florets; phyllaries narrowly lanceolate.

Geographical distribution: southern Brazil. A rather well marked series.

Pollen type: B. Pollen grains were examined from the following specimens:

Vernonia holosericea Mart. ex DC., BRAZIL: Goiás, *Anderson 10284* (NY). **V. pungens** Gardn., BRAZIL: Distrito Federal, *Santos 11353* (NY). **V. schwenkiaefolia** Mart. ex DC., BRAZIL: Goiás, *Anderson 10425* (NY). **V. stricta** Gardn. in Hook., BRAZIL, *Warming 1863–65* (NY). **V. subulata** Baker, BRAZIL: Minas Gerais, *Irwin, et al. 27943* (NY). **V. virgulata** Mart. ex DC., BRAZIL: Distrito Federal, *Irwin & Soderstrom 6097* (NY).

Subsection **Scorpioides** Ekman. *Ark. Bot.* **13**(15): 86. 1914. TYPE SPECIES: *Vernonia scorpioides* (Lam.) Pers.

Inflorescences cymose-scorpoid; heads sessile or nearly so, with or without bracteal leaves.

Geographical distribution: Mexico, Central America and the West Indies south into Argentina.

Chromosome numbers: based on $n = 17$.

Series **Scorpioides** S. B. Jones *ser. nov.*

Frutices vel parvae arbores; inflorescentiae cymoso-scorpioideae; capitula parva, 10–20 flosculis sessilibus, bracteis foliaceis nullis. TYPE SPECIES: *Vernonia scorpioides* (Lam.) Pers.

Shrubs to small trees; inflorescences conspicuously cymose-scorpoid (see Figs. 2a, 2b, & 2c); heads small, sessile or nearly so, crowded on the inflorescence branches, bracteal leaves absent, with ca. 10–20 florets.

Geographical distribution: From Mexico and the West Indies south into Argentina.

Pollen types: A & D. Pollen grains were examined from the following specimens:

(TYPE A) *Vernonia cainarachensis* Hieron., PERU: Loreto, *Hutchinson, et. al.* 6043 (MO). *V. diffusa* Less., BRAZIL: *Belém* 1881 (NY). *V. ignobilis* Less., BRAZIL: Minas Gerais, *Gardner* 4766 (NY). *V. megaphylla* Hieron., PERU: San Martín, *Belshaw* 3423 (NY). *V. scorpioides* (Lam.) Pers., PERU: La Libertad, *Sagástegui & Suarez* 2636 (GA).

(TYPE D) *Vernonia brachiata* Benth., COSTA RICA: San José, *Skutch* 2525 (NY); morphologically very similar to *V. cainarachensis* which has type A pollen; perhaps best placed here for now.

Series **Macrolepidae** Benth. & Hook. *Gen. Pl.* **2**: 229. 1873. TYPE SPECIES: *Vernonia chamaepeuce* Sch.-Bip.

Series *Macrocephalae* Benth. & Hook. *Gen. Pl.* **2**: 229. 1873.

Subsection *Sellowianae* Cabrera, *Darwiniana* **6**: 306. 1944.

Subsection *Laurifoliae* Cabrera, *Darwiniana* **6**: 350. 1944.

Herbaceous perennials, sometimes slightly woody; inflorescences often greatly reduced with a few large heads, scorpoid-cymose to spike-like, or sometimes paniculate to scorpoid-cymose with many relatively large heads (see Figs. 1f, 2b, 2d, 2g & 3a); heads large with 40 to 80 florets; phyllaries various, sometimes highly developed or modified.

Geographical distribution: Centered mainly in southern Brazil and extending south into Argentina.

Chromosome number: $n = 17$.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia arachniolepis Ekman & Dusén ex Malme, BRAZIL: Rio Grande do Sul, *Rambos 51790* (NY). **V. bardanoides** Less., BRAZIL: Distrito Federal, *Irwin, et al. 13110* (NY). **V. carduoides** Baker ex Mart., BRAZIL: Goiás, *Irwin, et al. 14308* (NY). **V. chamaepeuces** Sch.-Bip. ex Baker in Mart., BRAZIL: Goiás, *Irwin, et al. 1674a* (NY). **V. eriolepis** Gardn., BRAZIL: Paraná, *Hatschbach & de Haas 14523* (NY). **V. ixiamesis** Rusby, BOLIVIA, *Gardenas 2017* (NY). **V. lacunosa** Mart., BRAZIL: Minas Gerais, *Irwin, et al. 24693* (NY). **V. lappoides** Baker in Mart., BRAZIL: Goiás, *Irwin, et al. 13745* (NY). **V. laurifolia** DC., BOLIVIA, *Rusby 1617* (NY). **V. macrophylla** Less., BRAZIL: Minas Gerais, *Barreto 1461* (NY). **V. mansoana** Baker, BRAZIL: Mato Grosso, *Irwin, et al. 16542* (NY). **V. niederleinii** Hieron., BRAZIL: Paraná, *Hatschbach 21585* (NY). **V. onopordoides** Baker in Mart., BRAZIL: Goiás, *Irwin, et al. 13210* (NY). **V. pulverulenta** Baker in Mart., BRAZIL: Mato Grosso, *Ratter, et al. 1528* (NY). **V. radula** Mart. ex DC., BRAZIL: Minas Gerais, *Claussen 1804* (NY). **V. riedelii** Sch.-Bip. ex Baker in Mart., BRAZIL, *Pohl s.n. 1950* (NY). **V. sellowii** Less., PARAGUAY, *Hassler 9910* (NY). **V. westermanii** Ekman, BRAZIL: Paraná, *Dusén 16400* (NY). **V. zuccarini-ana** Mart. ex DC., BRAZIL: Mato Grosso, *Irwin, et al. 17315* (NY).

Series **Remotiflorae** (Cabrera) S. B. Jones, *stat. nov.*

Subsection *Remotiflorae* Cabrera, *Darwiniana* 6: 311. 1944. TYPE SPECIES: *Vernonia remotiflora* Rich.

Herbaceous perennials, sometimes slightly woody at the base; inflorescences cymose-scorpoid, with conspicuous foliaceous bracts (see Figs. 1e, 2e, 2f, 2g, & 3d); heads sessile or short-pedicellate, variously arranged on the branches.

Geographical distribution: Southern Brazil south into Argentina.

Chromosome numbers: $n = 17, 34, 51, 68$.

Pollen type: B. Pollen grains were examined from the following specimens:

Vernonia ammophila Gardn., BRAZIL: Goiás, *Irwin, et al. 31800* (NY). **V. brevipetiolata** Sch.-Bip. ex Mart., BRAZIL, *Hoehne 19101* (NY). **V. cordigera** Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 28283* (NY). **V. coriacea** Less., BRAZIL: Minas Gerais, *Irwin, et al. 27494* (NY). **V. cuiabensis** Baker in Mart., BRAZIL: Mato Grosso, *Irwin, et al. 16013* (NY). **V. dorsiventralis** Chod., PARAGUAY, *Hassler 3127* (NY). **V. elegans** Gardn., BRAZIL: Goiás, *Irwin, et al. 15201* (NY). **V. glabrata** Less., PARAGUAY, *Hassler 8117a* (NY). **V. hoveaefolia** Gardn., BRAZIL, *Gardner 3792* (NY). **V. laevigata** Mart., BRAZIL: Distrito Federal, *Irwin, et al. 11211* (NY). **V. ligulaefolia** Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 28162* (NY). **V. linearis** Spreng., BRAZIL: Distrito Federal, *Irwin, et al. 26566* (NY). **V. obscura** Less., BRAZIL, *Hoehne 16089* (NY). **V.**

obtusata Less., BRAZIL: Goiás, *Irwin, et al.* 24246 (NY). **V. octandra** Sch.-Bip., BRAZIL, *Pohl* 1588 (NY). **V. remotiflora** Rich., SURINAME, *Maguire, et al.* 54252 (NY). **V. rubricaulis** H. & B., ARGENTINA, *Ochoa* 1969-58 (GA). **V. rugulosa** Sch.-Bip. ex Baker in Mart., BRAZIL, *Pohl* 2909 (NY). **V. saltensis** Hieron., ARGENTINA: Trancas, *Schreiter* 7419 (NY). **V. squarrosa** Less., BRAZIL: São Paulo, *Mimura* 286 (NY). **V. syncephala** Sch.-Bip., BRAZIL, *Hoehne* 155 (NY). **V. tarijensis** Hieron., ARGENTINA: Orán, *Cabrera* 4154 (NY). **V. valenzuelae** Chod., ARGENTINA, *Rodriguey* 15 (NY). **V. venia** Rich., BRAZIL, *Martus* 238 (NY).

Series **Flexuosae** (Cabrera) S. B. Jones, *stat. nov.*

Subsection *Flexuosae* Cabrera, *Darwiniana* 6: 329. 1944. TYPE SPECIES: *Vernonia cognata* Less.

Subsection *Echioides* Cabrera, *Darwiniana* 6: 327. 1944.

Herbaceous perennials, stems usually unbranched to the inflorescence; inflorescences often reduced, bracteal leaves reduced or absent, heads arranged along the branches of the inflorescence (see Figures 2d, 2g, 3a, & 3b); heads numerous to more typically few, sessile; phyllaries lanceolate, apex acuminate-aristate; pappus usually white, sometimes straw-colored; achenes pubescent.

Geographical distribution: Southern Brazil south into Argentina.

Chromosome numbers: $n = 17, 34$.

Pollen types: C, D. Pollen grains were examined from the following specimens:

(TYPE C) **Vernonia buchtieni** Gleason, BOLIVIA: Santa Cruz, *Steinbach* 5286 (NY). **V. cognata** Less., BRAZIL: São Paulo, *Jones* 22625 (GA). **V. desertorum** Mart. ex DC., BRAZIL: Mato Grosso, *Argent* 6729 (NY). **V. flexuosa** Sims, URUGUAY: Santa Clara, *Gallinal, et al.* 2914 (NY). **V. herbacea** (Vell.) Rusby, BRAZIL: Distrito Federal, *Sucre* 756 (NY). **V. lepidifera** Chod., PARAGUAY, *Hassler* 8241 (NY). **V. obovata** Less., BRAZIL, *Gardner* 3255 (NY). **V. platensis** Less., PARAGUAY, *Archer* 4750 (NY). **V. propingua** Hieron., PARAGUAY, *Hassler* 8637 (NY). **V. sceptrum** Chod., PARAGUAY, *Hassler* 8095 (NY). **V. senencionea** Chod., PARAGUAY, *Hassler* 8316 (NY). **V. simplex** Less., BRAZIL: Mato Grosso, *Harley & Souza* 10163 (NY). **V. tricholepsis** DC., PARAGUAY, *Hassler* 5651 (NY).

(TYPE D) **Vernonia barbata** Less., BRAZIL, *Pohl* 3025 (NY). **V. dura** Mart., BRAZIL: Mato Grosso, *Irwin, et al.* 17436 (NY). **V. oxylepsis** Sch.-Bip. ex Baker in Mart., BRAZIL: São Paulo, *Leuderwaldt* 16228 (NY).

Series **Aureae** S. B. Jones, *ser. nov.*

Herbae perennes vel interdum suffrutices; inflorescentiae scorpioideo-paniculatae interdum multum diminutae; bracteae foliaceae plerumque praesentes sed saepe multum diminutae; capitula

10–25 flosculis; phyllaria acuta usque longiacuminata. TYPE SPECIES: *Vernonia aurea* Mart. ex DC.

Herbaceous perennials, sometimes becoming shrubby; inflorescences scorpioid-paniculate, sometimes greatly reduced, bracteal leaves usually present but often greatly reduced (see Fig. 2g); heads medium sized with 10–25 florets; phyllaries acute to long-acuminate.

Geographical distribution: Southern Brazil. Not an especially well marked morphological series but many were also grouped together by Baker (Fl. Brasil 6(2): 58. 1873).

Pollen type: D. Pollen grains were examined from the following specimens:

Vernonia arenaria Mart. ex DC., BRAZIL: Amazônas, Prance, et al. 2700 (NY). **V. aurea** Mart. ex DC., BRAZIL: Bahia, Irwin, et al. 14595 (NY). **V. eremophila** Mart. ex DC., BRAZIL: Distrito Federal, Irwin & Soderstrom 5939 (NY). **V. fruticulosa** Mart. ex DC., BRAZIL: Minas Gerais, Irwin, et al. 27705 (NY). **V. grisea** Baker, BRAZIL: Amazônas, Pires, et al. 5322 (NY). **V. hirtiflora** Sch.-Bip. ex Baker in Mart., BRAZIL, Pohl 3282 (NY). **V. subcordata** Gardn. ex Hook., BRAZIL: Minas Gerais, Irwin, et al. 28384 (NY).

Series **Canescentes** S. B. Jones, ser. nov.

Suffrutices vel raro herbae perennes; folia subtus pilosa; inflorescentiae scorpioideae, bracteis foliaceis grandis vel reductis; capitula mediocria 10–12 flosculis; phyllaria acuta. TYPE SPECIES: *Vernonia canescens* H.B.K.

Shrubs or very rarely herbaceous perennials; leaves softly pilose beneath; inflorescences scorpioid (see Figs. 1f, 2a, 2b, 2f, & 2g); heads medium sized, with 10–20 florets; bracteal leaves large or reduced.

Geographical distribution: Southern Mexico and Central America across northern South America and south along the Andes into Brazil. This series appears closely related to series *Scorpioides*.

Chemistry: glaucolide-B.

Chromosome number: $n = 17$. Pollen types: B & C. Pollen grains were examined from the following specimens:

(TYPE B) **Vernonia costata** Rusby, PERU: Cuzco, Vargas 14495 (US). **V. coulonii** Sch.-Bip. ex Baker in Mart., BRAZIL: Distrito Federal, Irwin & Soderstrom 5204 (NY). **V. deflexa** Rusby, BOLIVIA, Williams 1444 (NY). **V. densipaniculata** Rusby, BOLIVIA, Buchtien 1533 (NY). **V. geminata** Less., BRAZIL, Gardner 790 (NY). **V. helvphila** Mart., BRAZIL, Hoehne 16068 (NY). **V. micrantha** H.B.K., COLOMBIA, Sneidern 1559 (NY).

(TYPE C) *Vernonia araguensis* Badillo, VENEZUELA: Aragua, *Steyermark & Agostini 24* (NY). *V. araripensis* Gardn., GUYANA, *coll. ign. WB235* (NY). *V. canescens* H.B.K., PANAMA: Canal Zone, *Dressler 3425* (GA). *V. corrientensis* Ekman, PARAGUAY, *Hassler 2850* (NY). *V. cotoneaster* Less., VENEZUELA: Bolívar, *Wurdack 34412* (NY). *V. glandulosa* Badillo, VENEZUELA, *Foldats 2874* (NY). *V. gracilis* H.B.K., COLOMBIA: Atlántico, *Dugand & Jaramillo 2719* (NY). *V. lilacina* Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 20649* (NY). *V. miersiana* Gardn., BRAZIL: Mato Grosso, *Irwin, et al. 16983* (NY). *V. mollis* H.B.K., GUATEMALA: Alta Verapaz, *Steyermark 44039* (NY). *V. muricata* DC., BRAZIL: Santa Catarina, *Reitz & Klein 6521* (NY). *V. pari* Badillo, GUYANA, *Tate 306* (NY). *V. phyllostachya* Gleason, MÉXICO, *Arsène 1913* (NY). *V. pseudomollis* Gleason, PERU: Cuzco, *Vargas 412* (F). *V. salzmanni* DC., PERU: Santa Ana, *Cook & Gilbert 1466* (US). *V. tricephala* Gardn., TRINIDAD, *Britton & Broadway 2421* (NY). *V. virens* Sch.-Bip. ex Baker in Mart., BRAZIL: Mato Grosso, *Hunt & Ramos 5977* (NY).

Series **Foliatae** (Benth. & Hook.) S. B. Jones, *stat. nov.*

Subseries *Foliatae* (Benth. & Hook.) Gen. Pl. 2: 229. 1873. TYPE SPECIES:
Vernonia agyropappa Buek.

Shrubs, often scandent; leaves tending to be coriaceous, apex acute to long acuminate; inflorescences lax, of few to many spreading scorpioid-cymes (see Figures 2a, 2b, 2c, & 2e); heads may or may not be subtended by a bracteal leaf.

Geographical distribution: Mexico south through Central America into Peru.

Pollen type: B. Pollen grains were examined from the following specimens:

Vernonia agyropappa Buek, COSTA RICA, *Lems 5050* (NY). *V. ehretiaefolia* Benth., VENEZUELA: Bolívar, *Maguire & Wurdack 33939-A* (NY). *V. lehmannii* Hieron., COLOMBIA: Antioquia, *Barkley & Gutiérrez V. 1413* (NY). *V. myriocephala* DC., PERU: Junín, *Killip & Smith 26099* (NY). *V. polypleura* Blake, MÉXICO: Chiapas, *Mutuda 2067* (NY). *V. schiedeana* Less., BRITISH HONDURAS: Belize, *Dwyer, et al. 180* (NY). *V. seemanniana* Steetz in Seem., COSTA RICA: San José, *Skutch 4112* (NY). *V. tortuosa* (L.) Blake, MÉXICO: Veracruz, *Beaman 5623* (GA). *V. trilectorum* Gleason, COLOMBIA: Santander, *Killip & Smith 15374* (NY).

Series **Sagraeanae** (Ekman) S. B. Jones, *stat. nov.*

Subsection *Sagraeanae* Ekman. Ark. Bot. 13(15): 11. 1914. TYPE SPECIES:
Vernonia sagraeana DC.

Small shrubs; leaves membranaceous; inflorescences cymose-scorpioid, cymes elongate, with large bracteal leaves (see Figs. 1f, 2b, & 2g); heads rather large; involucre campanulate; achenes glabrous.

Geographical distribution: West Indies. A very natural series.

Pollen type: B. Pollen grains were examined from the following specimens:

Vernonia aronifolia Gleason, CUBA, *Shafer 13514* (F). **V. ekmanii** Urban, HAITI, *Ekman 5351* (US). **V. purpurata** Gleason, CUBA, *Ekman 9375* (NY). **V. sagraeana** DC., CUBA, *Ekman 10327* (GH). **V. sprengeliana** Sch.-Bip., HISPANIOLA, *Ekman 11618* (US). **V. viminalis** Gleason, CUBA, *Wright 285* (US). **V. wrightii** Sch.-Bip., CUBA, *Ekman 3370* (US).

Series **Arborescentes** (Ekman) S. B. Jones, *stat. nov.*

Subsection *Arborescentes* Ekman. *Ark. Bot.* **13**(15): 27. 1914. TYPE SPECIES:
Vernonia arborescens (L.) Sw.

Mostly small shrubs; inflorescences cymose-scorpioid, cymes elongate or greatly reduced (see Figs. 1e, 2f, & 2g); foliaceous bracteal leaves.

Geographical distribution: West Indies. Appears closely related to other series of subsection *Scorpioides* from South America.

Chromosome number: $n = 17$.

Pollen types: B & C with a few species having a grain intermediate between B. and C. Pollen grains were examined from the following specimens:

(TYPE C) **Vernonia acuminata** Less., JAMAICA, *Howard & Proctor 13371* (GA). **V. albicaulis** Pers., ST. KITTS, *Proctor 18501* (US). **V. arborescens** (L.) Sw., ST. VINCENT, *Smith & Smith 359* (GH). **V. arbuscula** Less., BAHAMAS, *Wight 70* (F). **V. commutata** Ekman, CUBA, *Clemente 668* (NY). **V. complicata** Wright ex Griseb., CUBA, *Britton 2225* (F). **V. desiliens** Gleason, CUBA, *Alain & Figuiera 4792* (NY). **V. fructicosa** (L.) Sw., HISPANIOLA, *Ekman 2251a* (NY). **V. harrisii** S. Moore, JAMAICA, *Proctor 2168* (TEX). **V. leptoclada** Sch.-Bip., CUBA, *Shafer 8408* (F). **V. orbicularis** Alain, CUBA, *Webster 3873* (GH). **V. pineticola** Gleason, CUBA, *Ekman 10286* (GH). **V. segregata** Gleason, CUBA, *Acunae 12799* (US). **V. sericea** Rich., HISPANIOLA, *Leonard 8096* (US). **V. stenophylla** Less., CUBA, *Ekman 4050* (US). **V. urbaniana** Ekman ex Urban, CUBA, *Ekman 10083* (F). **V. verticillata** Proctor ex Adams, JAMAICA, *Keeley & Keeley 1250* (GA).

(TYPE B) **Vernonia borinquensis** Urban, PUERTO RICO, *Heller 4391* (F).

(TYPE B-C) **Vernonia pluvialis** Gleason, JAMAICA, *Maxon 9786* (NY). **V. trinitatis** Ekman, TRINIDAD, *Keeley & Keeley 1946* (GA).

Series **Pallescentes** (Ekman) S. B. Jones, *stat. nov.*

Subsection *Pallescentes* Ekman. *Ark. Bot.* **13**(15): 88. 1914. TYPE SPECIES:
Vernonia pallescens Gleason.

Erect shrub; leaves membranaceous; inflorescences scorpioid-cymose, cymes elongate and sometimes dichotomously branched

(see Fig. 2a); pappus bristles of outer series filiform and subequal with inner series.

Geographical distribution: St. Vincent in the West Indies.

Pollen type: C. Pollen grains were examined from the following specimen:

Vernonia pallescens Gleason, B.W.I.: St. Vincent, *Howard & Howard 18011* (GH).

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